Population connectivity of an overexploited coastal fish, Argyrosomus coronus (Sciaenidae), in an ocean-warming hotspot

Henriques, R.; Potts, W. M.; Santos, C. V.; Sauer, W. H. H.; Shaw, Paul

Published in:
African Journal of Marine Science

DOI:
10.2989/1814232X.2018.1434090

Publication date:
2018

Citation for published version (APA):
Henriques, R., Potts, W. M., Santos, C. V., Sauer, W. H. H., & Shaw, P. (2018). Population connectivity of an overexploited coastal fish, Argyrosomus coronus (Sciaenidae), in an ocean-warming hotspot. *African Journal of Marine Science*, *40*(1), 13-24. https://doi.org/10.2989/1814232X.2018.1434090

Title: Population connectivity of an overexploited coastal fish (*Argyrosomus coronus* Griffiths and Hecht, 1995) in an ocean warming hotspot

Authors: Romina Henriques[1,2], Warren M. Potts[2], Carmen V. Santos[3], Warwick H.H. Sauer[2], Paul W. Shaw[4,2]

[1]Evolutionary Genomics Group, Department of Botany and Zoology, University of Stellenbosch, Stellenbosch, South Africa;

[2]Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa;

[3]Faculdade de Ciências da Universidade Agostinho Neto (FCUAN), Luanda, Angola;

[4]Institute of Biological, Environmental & Rural Sciences, Aberystwyth University, Aberystwyth, UK.

Corresponding author: Romina Henriques

Evolutionary Genomics Group

Department of Botany and Zoology

University of Stellenbosch

Private Bag X1

Matieland 7602

South Africa

tel: +27 21 808 3229

fax: +27 21 808 2405

email: rhenriques@sun.ac.za

Abstract

Argyrosomus coronus is a commercially exploited fish with a distribution confined to the Angola-Benguela Frontal Zone (ABFZ), in the southeastern Atlantic. A previous study revealed that during a recent period of local warming the species has extended its distribution into Namibian waters, where it hybridized with resident and congeneric *A. inodorus*. Environmental changes are one of the major threats to marine biodiversity, and when combined with over-fishing have the potential to accelerate the decline of species. However, little is known regarding the evolutionary history and population structure of *A. coronus* across the ABFZ. We investigated genetic diversity, population structure and historical demographic changes using mtDNA Control Region sequences and genotypes at six nuclear microsatellite loci for 180 individuals. A single, genetically homogeneous population was indicated across *A. coronus* distribution range (ϕ_{ST} = 0.041, F_{ST} = 0.000, D = 0.000; p>0.05). These results imply that the oceanographic features within the ABFZ do not appear to influence population connectivity in *A. coronus*, simplifying the management of the species. However, reconstruction of demographic history points to a close link between the evolutionary history of *A. coronus* and the characteristics of the ABFZ. This finding highlights the vulnerability of this species to the rapid environmental changes being observed across this region, and indicates a pressing need for transboundary management to mitigate potential impacts of climate change in this global hotspot of seawater temperature changes.

Keywords: Angola-Benguela Frontal Zone, climate change, demographic history, fisheries, population structure, Sciaenidae

Introduction

Anthropogenic activities are recognized to have significant impacts in marine systems at multiple levels, ranging from habitat disturbance (Pauly et al. 2005) to overfishing (Sala and Knowlton 2006) and loss of genetic diversity (Pinsky and Palumbi 2014). Exploitation and harvesting in particular are known to strongly influence fish populations and their associated ecosystems (Pauly et al. 2005), which in combination with on-going climate change can have compound effects on the viability and long-term survival of marine fishes (Last et al. 2011). Species can react to the impacts of climate change either by shifting their distributional range or by adapting to changing conditions through individual ecological plasticity and/or local population adaptation (Briggs 2011; Last et al. 2011). However, since ecological plasticity and local adaptation have strong genetic components, over-harvesting has the potential to impact the long-term adaptive ability of marine fishes by decreasing extant genetic diversity (Allendorf et al. 2014). Therefore, understanding the impact of exploitation on genetic diversity and population sub-structuring is critical for predicting the likely consequences of continued exploitation and climate change.

Global warming hotspots are defined as regions with above average increases in ocean temperature (Hobday and Pecl 2014). A number of ocean warming hotspots have been identified throughout the world, including one in the coastal waters off southern Angola (Hobday and Pecl 2014). From an oceanographic perspective, this region is dominated by the Angola-Benguela Frontal Zone (ABFZ) off the coast of central Angola (~16^{o}S), which results from the convergence of the warm-tropical Angola Current and the cold, upwelling dominated Benguela Current (Kirkman et al. 2016). This is a highly dynamic environment, with the position and strength of the ABFZ varying throughout the year in response to changes in the Southern Atlantic Anticyclone (SAA) and the upwelling regime of the Benguela Current (Jahn et al. 2003). During summer, the ABFZ is displaced southwards due

74 to the expansion of the SAA (up to 18^{o}S), while in winter the contraction of the SAA and
75 increased upwelling off Namibia results in a northward movement of the front (to 13^{o}S; Jahn
76 et al. 2003). Despite the environmental and biological complexity of this area, few studies
77 have investigated the impact of contemporary environmental changes at a regional level
78 (Monteiro et al. 2008; Potts et al. 2009; 2010; 2014), with the region remaining largely
79 understudied.

80 In the last two decades, the ABFZ region has experienced a rapid increase in sea surface
81 temperatures (SSTs; Monteiro et al. 2008), which has already impacted distribution ranges of
82 local species such as the sciaenid fish *Argyrosmus coronus* Griffiths & Hecht, 1995 (Potts et
83 al. 2014). This coastal, migratory species has a distribution range extending from northern
84 Angola to northern Namibia (Griffiths and Heemstra 1995; Potts et al. 2010), and is a
85 valuable fishery resource targeted by recreational, artisanal and subsistence fisheries (Potts et
86 al. 2009; 2010). Despite sustaining a multi-user fishery, there are currently no specific fishing
87 regulations for *A. coronus* in Angola. The Angolan Presidential Decree 11/2016 (available
88 upon request) groups it into "Sciaenid" fishes, which are managed as a quota. In particular,
89 subsistence and recreational catches, which constitute the main fishing effort in the region,
90 are not regularly monitored nor included in the yearly total capture allowance. Therefore, the
91 species is effectively not managed at present and increasing fishing efforts in the region
92 (Potts et al. 2009) have resulted in population collapse (Beckensteiner et al. 2016).

93 A previous life history study suggested that the distribution range of *A. coronus* is closely
94 linked with the seasonal displacement of the ABFZ, with adults undertaking a seasonal
95 alongshore migration, and spawning thought to occur in the southern region of its range
96 during late spring and summer (Potts et al. 2010). Recent findings, however, seem to dispute
97 this hypothesis, with ripe and running females observed on an offshore reef in 10 m of water
98 near the Kwanza Estuary (northern Angola) during the austral winter months (Potts,

unpublished data). Therefore, the full extent of the spawning locations of the species remains unknown. The duration of the pelagic egg and larval stage is also unknown, although it is expected to be similar (~26 days) to that of the sister species, *Argyrosomus japonicus* (Edworthy et al. submitted). Juveniles (300 – 600 mm Total Length - TL) and subadults (601 – 870 mm TL) are thought to be resident, with maturation (~870 mm TL) heralding the migratory phase (Potts et al. 2010). Growth is rapid, with fish attaining maturity at just four years of age (Potts et al. 2010).

The rapidly increasing SSTs in the region have coincided with a southwards distributional shift of *A. coronus* into central Namibia, where it now overlaps and has begun hybridizing with the congeneric *A. inodorus* (Potts et al. 2014). Anthropogenic-mediated hybridization increasingly has been reported in the marine environment, either due to habitat degradation (Mullen et al. 2012), species introduction (Coleman et al. 2014) or environmental changes (Potts et al. 2014), and has the potential to erode genetic diversity and change the evolutionary history of species (Roberts et al. 2009; 2010).

The aim of this study was to examine genetic diversity and population sub-structure of exploited *A. coronus* in order to gain an understanding of the distribution of the species in relation to the ABFZ. To do this, we employed both mitochondrial DNA (mtDNA) and nuclear microsatellite DNA markers to assess: i) levels of genetic diversity in *A. coronus* throughout its present range; ii) the influence of the oceanographic features of the ABFZ in population sub-structuring; and iii) the demographic and evolutionary history of the species in the region.

Methods

Sampling and laboratory analyses

123 Sampling was conducted during the austral winter month of June from 2007 to 2010,
124 at five locations spanning the ABFZ region (Figure 1). Although spawning grounds and
125 nursery areas remain mainly undescribed, previous work on species biology suggests that
126 spawning occurs in the south of Angola from late austral spring to early summer (Potts et al.
127 2010) and in the north during the austral winter (Potts, unpublished data). Therefore,
128 sampling during the same season throughout the distribution range will likely maximize the
129 possibility of capturing individuals representing the full diversity of the species. A fin clip
130 was removed immediately after capture and preserved in 95% ethanol. Total genomic DNA
131 was extracted using a standard phenol : chloroform method (Sambrook et al. 1989).
132 Assessment of genetic variation within and between sampling sites was performed
133 using both mitochondrial (mtDNA) and nuclear (nDNA) markers. The mtDNA Control
134 Region (CR) was amplified by Polymerase Chain Reaction (PCR) and sequenced for a sub-
135 set of samples (12 per sampling site), using a universal primer pair following the original
136 protocol (Apte and Gardner 2002). Obtained sequences were visually inspected and aligned
137 in BIOEDIT 7.0.5 (Hall 1999) using CLUSTAL X (Thompson et al. 1997). To test for
138 deviations to the expectation of neutrality we calculated Tajima's *D* (Tajima 1989) and Fu's
139 F_S (Fu 1997) summary statistics in ARLEQUIN 3.5 (Excoffier et al. 2005). The most suitable
140 nucleotide substitution model was estimated in jMODELTEST 0.1 (Posada 2008), under the
141 AIC approach, and used in subsequent analyses.
142 Six cross-specific nDNA microsatellite primer pairs developed for the sister species
143 *Argyrosomus japonicus* (UBA5, UBA40, UBA50, UBA91, UBA853 and UBA854 –
144 Archangi et al. 2009) were amplified following the original protocol. Microsatellite
145 amplicons were genotyped in an ABI 3500 (Applied Biosystems, UK) using LIZ-600® as an
146 internal size marker, and scored based on size in GENEMAPPER 4.0 (ABIPrism). In order to
147 ensure accurate allele size scoring, we scored the same reference individuals across multiple

runs. The quality of the microsatellite dataset was evaluated by estimating the occurrence of stuttering and large allele dropout in MICROCHECKER (van Oosterhout et al. 2006), and null allele frequencies in FREENA (Chapuis and Estoup, 2007). Obtained genotypic frequencies were tested for deviations from Hardy-Weinberg and linkage expectations in GENEPOP 4.2 (Raymond and Rousset 1995).

Genetic diversity and population sub-structuring of A. coronus across the ABFZ region

Overall and intra-sample levels of genetic diversity were estimated as number of haplotypes (H), number of private haplotypes (PH), and haplotype (*h*) and nucleotide diversity (π) for the mtDNA dataset in ARLEQUIN 3.5 (Excoffier et al. 2005), and number of alleles (Na), allelic richness (AR), observed (H_O) and expected (H_E) heterozygosity and Wright's inbreeding coefficient (F_{IS}), for the microsatellite dataset in FSTAT 2.9.3 (Goudet 1995). In addition, the distribution of microsatellite allelic frequencies per locus and sampling region were calculated in the R package gstudio. Due to sampling restrictions, resulting in limited sample sizes, and the cross-specific nature of the microsatellite loci, we conducted a preliminary analysis to investigate statistical power of marker variability to infer population structure. Simulations were performed in POWSIM 4.1 (Ryman and Palm 2006) for six loci and two populations representing minimum and maximum sample sizes (N = 26 and N = 40), for five levels of postulated genetic differentiation (F_{ST} = 0.002, F_{ST} = 0.005, F_{ST} = 0.01, F_{ST} = 0.02 and F_{ST} = 0.05), using a combination of effective population size (N_e = 3000) and time since divergence (t = 10; t = 30, t = 70, t = 125, t = 310 generations since isolation). Each simulation ran for 10 000 replicates, and power was estimated as the proportion of exact tests that indicated significant differentiation.

Haplotype networks were constructed in NETWORK 5.0.0.0 (Bandelt et al. 1999) to investigate the geographical distribution of mtDNA haplotypes, using the Median-Joining

spanning network algorithm with the maximum parsimony post-processing option enforced to help solve ambiguous connections. The shortest tree was chosen using a coalescent theory approach (Grant and Bowen 2006).

Levels of pairwise genetic differentiation between samples and across the whole dataset were estimated using ϕ_{ST} in ARLEQUIN 3.5 (Excoffier et al. 2005) for mtDNA, and Weir & Cockerham's F_{ST} estimator (Weir and Cockerham 1984) in FSTAT 2.9.3 (Goudet 1995) and Jost's D (Jost 2008) in SMOGD (Crawford 2010) for nDNA, with statistical significance assessed after 10 000 permutations. In addition, a hierarchical analysis of molecular variance (AMOVA) was performed for both datasets to test two hypotheses: i) population differentiation in *A. coronus* is associated with the position of the ABFZ at the time of sampling (LUA, LUC, FLA vs. CUN, HEN); ii) population differentiation is associated with the temporal nature of the sampling strategy: (2007 FLA & CUN vs. 2009 LUC & HEN vs. 2010 LUA). All AMOVA tests were performed in ARLEQUIN 3.5 (Excoffier et al. 2005), and statistical significance was assessed after 10 000 permutations. Furthermore, we investigated the potential for the presence within the dataset of mixtures of individuals from differentiated sub-populations of *A. coronus* by testing the spatial distribution and clustering of genotypes using a factorial component analysis in GENETIX 4.0.5 (FCA – Belkhir et al. 2000), and by employing the approach of STRUCTURE 2.3.4 (Pritchard et al. 2000). Simulations were performed under the admixture model, with correlated allele frequencies, and allowing the number of clusters to vary between 1 and 5 (K = 1 to 5). Five independent runs were performed for each K to ensure convergence, and estimation of the most likely K followed the method of Evanno et al. (2005), in STRUCTURE HARVESTER 0.6.94 (Earl et al. 2012).

Demographic history of A. coronus

As no significant between-sample differentiation was observed (see Results), assessment of *A. coronus* demographic history was performed using all samples pooled to generate a more representative sample size. Summary statistics (h, π, Tajima's D and Fu's F_S) and mismatch distribution analyses were performed in ARLEQUIN 3.5 (Excoffier et al. 2005) for the CR dataset. Significant deviations from the hypothesis of past demographic expansion were assessed using the sum of squared differences (SSD) test, after 10 000 permutations. Estimates of time since expansion (τ) were obtained using the mismatch distribution parameters, after $\tau = 2\mu t$. Given the uncertainty regarding mutation rates (μ), we used three different values to estimate demographic parameters: i) μ = 3.6% per million years (MY, conservative mutation rate derived from an ancient speciation event in marine fishes due to the closure of the Isthmus of Panama – Donaldson and Wilson 1999); ii) μ = 5% per MY (a mid-point estimate); and iii) μ = 10% per MY (a faster mutation rate derived from a shallow and more recent divergence event in Atlantic pygmy angelfishes – Bowen et al. 2006) with generation time (t) estimated at 4.3 years for females (Potts et al. 2010). In addition, a Bayesian Skyline Plot (BSP) was performed in BEAST 1.8 (Drummond and Rambaut 2007) to examine historical changes in the female effective population size (N_{ef}). We performed three independent runs, using the piece-wise constant method for population expansion, for 50 million MCMC steps, sampling every 5 000 steps, under a strict molecular clock. Convergence of runs, BSP estimates and 95% highest posterior density (HPD) intervals were assessed in TRACER 1.6 (Rambaut and Drummond 2007).

As effective population size is a good estimator of relative recruitment levels in marine species (Carvalho and Hauser 1994), we used the microsatellite dataset to assess current N_e. Point estimates of N_e were performed using the linkage disequilibrium approach implemented in NeEstimator (Do et al. 2014), at the 0.05 critical allele frequency. Confidence intervals were assessed using a pairwise jack-knife approach.

Results

Genetic diversity and population differentiation in A. coronus across the ABFZ region

Given the hypervariablity of the mtDNA CR marker, a 524bp fragment was amplified for a subset of 60 individuals (12 per sampling site), displaying 46 variable sites resulting in 47 haplotypes (Table 1). The Tamura-Nei nucleotide substitution model (Tamura and Nei 1993), with variable rates among lineages ($\alpha = 0.613$), was identified as the most suitable model of sequence evolution and used in subsequent analyses. Significant deviations from the expectation of neutrality were detected for all sampling sites with Fu's F_S, but not with Tajima's D (Table 1). However, both metrics were significantly different from zero when the entire dataset was combined (Table 1). Overall, haplotype and nucleotide diversity were high ($h = 0.990$, $\pi = 0.010$; Table 1), and varied between $h = 0.970$ and $h = 1.000$ (LUC and CUN), and $\pi = 0.008$ and $\pi = 0.014$ (LUA and CUN).

There was no evidence of amplification errors and the microsatellite genotype frequencies conformed to Hardy-Weinberg and linkage equilibrium expectations of random-mating across loci and samples (Table 2). Overall, nDNA genetic diversity was high ($H_O = 0.716$, $H_E = 0.734$), and ranged between $H_E = 0.718$ and $H_E = 0.731$ (FLA and CUN, respectively; Table 2). The number of alleles and allelic richness did not vary between samples (Na = 10, AR ~9), with the exception of LUA which exhibited the lowest values (Table 2). Distribution of allelic frequencies per locus and population did not reveal obvious differences between sampling sites (Supplementary Figure S1). Assessment of the power of the dataset to detect genetic differentiation between samples indicated that the six cross-specific loci used in this study could potentially detect differentiation as low as $F_{ST} = 0.01$ for populations samples of N = 26 – 40 in 85.5% of tests (100% of tests for $F_{ST} = 0.05$ and F_{ST} =

247 0.02), suggesting that these markers provided acceptable power for detecting relevant levels
248 of differentiation within the *A. coronus* population.

249 The null hypothesis of genetic homogeneity within the *A. coronus* population across the
250 ABFZ region could not be rejected, regardless of the dataset and analysis used. Network
251 analyses did not indicate obvious geographical sub-structuring either by frequency or
252 ancestral relatedness of mtDNA haplotypes in *A. coronus*: the majority of individuals were
253 represented by unique haplotypes, with a high frequency of private haplotypes within
254 samples but which were mostly singletons with no association of related singletons within
255 particular samples, while more abundant shared haplotypes were equally frequent among
256 sites (Figure 2). Overall levels of genetic differentiation among samples were low and non-
257 significant (mtDNA ϕ_{ST} = 0.041, nDNA F_{ST} = 0.000, nDNA D = 0.000; p>0.05), with
258 pairwise values between samples all very low and not significantly different from zero (Table
259 3). Similarly, the hierarchical analyses of molecular variance (AMOVA) did not detect
260 distinct sub-structuring for either hypothesis tested, with the majority of variance found
261 within samples and not between groups (Table 4). Assessment of cryptic genetic structuring
262 (clustering of genotypes) within the microsatellite dataset did not reveal any hidden patterns
263 of genetic differentiation across the ABFZ region: the FCA displayed a single cluster of
264 genotypes, despite some outlier individuals (Figure 3). Although the method of Evanno et al.
265 (2005) suggested K=2 as the most likely number of clusters (DeltaK = 15.987 – see
266 Supplementary material S1, Table S1), STRUCTURE plots for K=2 were admixed, with the
267 probability of belonging to each cluster being roughly 50% for every individual
268 (Supplementary material S1, Figure S1). The most likely explanation for this resides in the
269 inability to calculate DeltaK for K=1 (Supplementary material S1, Table S1). Therefore,
270 STRUCTURE analyses suggest the presence of one population, as this hypothesis had the

highest likelihood of all K tested (K=1, LnP(D) = -3910.70, Supplementary material S1 – Figure S2).

Demographic history

The negative and significant results from sequence evolution neutrality tests (Fu's F_S), combined with the inability to reject the null hypothesis of a sudden population expansion using mismatch distribution analyses (Figure 4) and the retrieved Skyline Plots (Figure 5), all point to the occurrence of a past population expansion in *A. coronus*. Estimates of time since expansion based on mismatch distribution parameters put expansion date between 11 and 31 thousand years ago (KY – Figure 4), depending on the mutation rate used. Similarly, the Skyline Plot approach revealed the occurrence of a steep increase in female effective population size circa ~25-70 KY (Figure 5), depending on the mutation rate used and despite the broad 95% HPD.

Assessment of current effective population size, based on the microsatellite dataset, revealed that *A. coronus* exhibits moderately large long-term effective population sizes (N_e = 3 307; 95% CI: 322 - ∞).

Discussion

Genetic diversity, population structure and phylogeographic patterns of A. coronus across the ABFZ

In recent years, intense fishing pressure has been linked in several marine fishes to reduced population sizes (Briggs 2011), shifts in size ranges and age structures (Miethe et al. 2010), and perhaps most importantly to loss of genetic diversity (Pinsky and Palumbi 2014; Henriques et al. 2016). In a changing environment, the loss of genetic diversity is of great concern, as it will influence the ability of a species to adapt to future changes (Briggs 2011).

296 Despite the previously reported high levels of exploitation and reduced population size of *A.*
297 *coronus*, where the Egg-per-Recruit measure of abundance was estimated at less than 10% of
298 the value in the absence of fishing for the period 2005-2013 (Beckensteiner et al. 2016), the
299 historical and present levels of genetic diversity in this species were found to be high and
300 similar in range to those reported for other sciaenid species not only from the same region
301 (Henriques et al. 2014; 2015) but also to those occurring in more stable environments
302 (Silberschneider and Gray 2008; Diaz-Jaimes et al. 2010). The results presented here suggest
303 that overfishing does not appear to have had (yet) a strong impact on contemporary levels of
304 genetic diversity in *A. coronus*.

305 Patterns of population genetic diversity and phylogeography indicated by both
306 mitochondrial and nuclear microsatellite DNA markers could not reject the hypothesis that *A.*
307 *coronus* comprises a single genetically homogeneous population across its complete range
308 within the ABFZ region, suggesting that there are no barriers to dispersal or interbreeding
309 (i.e. panmixia) of this species across this region. However, due to difficulties in accessing
310 large samples of the study species from such an inaccessible area, sample sizes were below
311 the recommended 50 individuals per sampling site (Cornuet et al. 1999): therefore it is
312 possible that small sample sizes and hypervariability of the markers used could have
313 decreased resolution power for detecting subtle population sub-structuring if present. For
314 example, the high haplotype diversity observed for the mtDNA dataset might reduce power to
315 statistically test differentiation as the majority of individual possessed unique haplotypes.
316 However, phylogeographic theory predicts that sub-structuring of populations would result in
317 non-random geographical clustering of related haplotypes (Avise 2000). In contrast, our
318 results show haplotypes private to individual samples are most closely related to haplotypes
319 private to other samples, interconnected throughout the phylogeographic network without an
320 obvious geographical clustering pattern, consistent with random dispersion of *A. coronus*

throughout the entire distribution range and similar to patterns observed in other abundant marine fish species with high gene flow (e.g. McKeown et al. 2015).

For the nDNA microsatellite allelic distributions, POWSIM analyses indicated that the dataset had suitable power to detect genetic differentiation as low as F_{ST} = 0.01 in 85.5% of the tests, with power decreasing to 41% for F_{ST} = 0.005. The combination of the observed results does not allow to reject the null hypothesis of genetic homogeneity in this species. In fact, several lines of evidence support potential panmixia, as the microsatellite loci had the ability to detect even weak genetic sub-structuring (F_{ST} > 0.01), and revealed very low levels of population divergence (global F_{ST} = 0.000, inter-sample F_{ST} = 0.000 – 0.005). Furthermore, there was no evidence of cryptic genetic structuring within samples, as no deviations to Hardy-Weinberg or linkage equilibrium were observed, which might have indicated the presence of a Wahlund effect (Nei and Li 1973; Pusack et al. 2014; Henriques et al. 2017). Finally, both FCA and STRUCTURE clustering analyses supported the presence of one gene pool, even though STRUCTURE may have less power to detect sub-structuring if F_{ST} < 0.02 (Latch et al. 2006). Therefore, the most likely scenario is that *A. coronus* is composed by one population throughout its distribution range. Resolution of spatial stock structure at a finer scale may be beyond the level of neutral genetic markers and benefit from complementary analysis of markers under selection (Canino et al. 2005).

Major oceanographic features across the wider Benguela Current region have been shown as barriers to effective dispersal of marine taxa, with many species exhibiting distinct genetic divergence between populations indicating breakdown of interbreeding and gene flow (Henriques et al. 2012; 2016; von der Heyden et al. 2008; 2011). However, the potential of an oceanographic feature to be a barrier to gene flow is closely linked to the biological features of the species itself (Galarza et al. 2009; Luiz et al. 2012). *Argyrosomus coronus* is a relatively long-lived (max = 13 years), benthopelagic sciaenid that appears to undertake

346 seasonal alongshore migrations (Potts et al. 2010). Catch-per-effort data indicate that this
347 species is predominantly found in a temperature range of 16 – 22ºC, similar to the SST range
348 around the ABFZ, and that the seasonal movement patterns of this frontal zone are thought to
349 be the driver of *A. coronus* migratory behaviour (Potts et al. 2010; 2014). Recent biological
350 findings suggest that spawning may occur throughout the distribution range, with ripe and
351 running females found off northern Angolan waters during the austral winter (June – Potts,
352 unpublished data), and a protracted spawning period documented for the southern region,
353 extending from late spring to summer (Potts et al. 2010). Based on these findings and the
354 seasonal shifts of the ABFZ, it is possible that spawning only occurs during a narrow thermal
355 window. Indeed, spawning in the sister species *A. japonicus* off South Africa occurs only
356 when temperatures are within a narrow range (20 – 24°C; Griffiths, 1996). These findings
357 may suggest that *A. coronus* has multiple spawning grounds distributed throughout the
358 system, with spawning regulated by the marked seasonal and regional SST patterns (Jahn et
359 al. 2003). Besides the appropriated thermal range, the timing and location of spawning may
360 also have evolved to maximize the dispersal of pelagic eggs and larvae in this highly unstable
361 habitat (Potts et al. 2010). *Arygyrosomus coronus*, like *A. japonicus*, is thought to use
362 estuaries as nursery grounds (Griffiths 1996; Potts et al. 2010). By migrating and reproducing
363 in the south of their distribution during the spring-summer, pelagic eggs and larvae can be
364 passively transported to the Cunene Estuary, through the seasonal displacement of the ABFZ.
365 Similarly, by reproducing in the northern region during winter when SSTs are cooler, eggs
366 and larvae can be passively dispersed northwards towards nursery grounds in the large
367 estuaries (e.g. Kwanza, Congo) to the north. Indeed, juvenile specimens (185 – 285 mm TL)
368 have been observed as far north as Gabon (Poll 1954). Interestingly, an on-going
369 conventional tagging study has revealed that movement may occur during the late juvenile
370 stage (400 – 600 mm TL), with individuals dispersing up to 210km, and during the adult

stage with individuals migrating 750 km (Parkinson et al., unpublished data). The tagging studies thus suggest that *A. coronus* is capable of dispersal throughout much of its life cycle, which may explain the observed genetic homogeneity of the species across the ABFZ region.

Demographic history of A. coronus

The demographic history of *A. coronus* shows evidence for past population size changes that appear to be linked with historical climatic shifts in the region. Results from the mtDNA analyses revealed evidence for a past population expansion approximately 11-75 KY (depending on the mutation rate used) around or just pre-dating the Last Glacial Maximum (LGM; Clark et al. 2009). Although estimates of time since expansion should be regarded with caution due to the assumptions required for calibration of the molecular clock, both the mismatch distribution and the coalescent-based analyses depicted a clear population increase in the last 25-75 KY. The expansion in *A. coronus* appears to have occurred earlier in time than those reported for other fishes (Grant and Bowen 2006), but is similar in range to those suggested for *Atractoscion aequidens* (currently *A. microlepis*) and *Merluccius capensis* in the same region (Henriques et al. 2014; 2016).

During the Quaternary, the Benguela Current experienced increased upwelling events and colder SSTs, particular around 60 KY and 18 KY (Kirst et al. 1999). Climatic changes in the Pleistocene are thought to have influenced the genetic signatures of the populations of several marine fishes, particularly in the southeastern Atlantic, with several population expansions dating from the Holocene (8-6 KY; e.g. Matthee et al. 2007; von der Heyden et al. 2007; 2010). In the case of *A. coronus*, it appears that the population survived the LGM (in possible glacial refugia) after which expansion began from early during the warming process. Similar refugial hypotheses have been suggested to have contributed to an earlier population expansion of *A. aequidens* in the northern Benguela (Henriques et al. 2014), and in other

396 temperate species from the Atlantic Ocean (Francisco et al. 2011; Faria et al. 2012). With
397 temperature requirements that overlap with those found in the ABFZ (Potts et al. 2010), it is
398 likely that changes in the range of the frontal system would be mirrored by changes in the
399 distribution and abundance of *A. coronus*. Indeed, recent rapid warming in the southern
400 Angola region has coincided with a decrease in the abundance of this species in the region,
401 and an increase (when compared with *A. inodorus*) in the cooler waters off central and
402 northern Namibia (Potts et al. 2014). Such distributional shifts associated with changing
403 temperatures are thought to be one of the first consequences of climate changes in multiple
404 species (Grant and Bowen 2006; Garroway et al. 2011; Hill et al. 2011).

405 Estimates of long-term effective population sizes, based on the microsatellite dataset,
406 showed values well above the minimum threshold for maintenance of a species' evolutionary
407 potential (N_e > 500, Frankham 2005), and with no evidence for recent population contraction.
408 This implies that exploitation has not impacted the genetic diversity of *A. coronus*, despite a
409 recent study suggesting that the population is at 5-10% of its pristine biomass (Beckensteiner
410 et al. 2016). Such findings are likely to result from historically high effective population sizes
411 and diversity levels, where only severe and long-term population crashes would result in a
412 large and detectable loss (Riccioni et al. 2010). However, these results should only be
413 interpreted as exploratory, as the observed upper bound of the 95% confidence interval was
414 infinity, suggesting that the dataset had limited power to define N_e accurately (Waples and
415 Do 2010), and further studies should be performed employing a higher number of markers
416 and larger sample sizes to investigate contemporary changes in N_e.

417

418 ***Conclusions and implications for understanding climate change effects and sustainable***
419 ***harvesting***

The results from this study combined with the findings of Potts et al. (2010; 2014) suggest that the evolutionary history of *A. coronus* is strongly linked with the characteristics of the ABFZ. The inability to reject the null hypothesis of genetic homogeneity, leading to a conclusion of widespread panmixia may be a consequence of the adaptation to, and colonization of, the frontal system itself by *A. coronus*. The observed spawning behavior and possible annual return migration appear to correlate to the movement of the ABFZ and thus climatic changes that affect its oscillatory pattern may have a direct impact on the distribution range and population dynamics of *A. coronus.* Future studies should be conducted using not only neutral but also adaptive markers to investigate the possibility of cryptic genetic differentiation linked to local adaptation. Furthermore, the recent hybridization and introgression with *A. inodorus* in Namibia (Potts et al. 2014) deserves further research attention and continuous genetic surveys are required to understand the impacts of such hybridization events in the genomic architecture of both species.

The observed poleward range shift by *A. coronus* will also have a significant impact in the fishing industry of the region. Fishing policies differ between Angola and Namibia, and since both *Argyrosomus* species have significantly different life-history traits (Holtzhausen et al. 2001; Potts et al. 2010) a transboundary fishing policy is urgently required. The Benguela Current Convention (BCC) has the mandate to coordinate fishing management policies across the Benguela Current region, aided in this endeavor through the Convention signed by South Africa, Namibia and Angola, which seeks to promote a coordinate regional approach to the long-term conservation, protection, rehabilitation, enhancement and sustainable use of the Benguela Current Large Marine Ecosystem. The BCC should thus both initiate and be involved in the establishment of future management plans for *A. coronus*.

Acknowledgements

445 The present work and R. Henriques were supported by a Fundação da Ciência e Tecnologia –
446 FCT grant (ref. SFRH/BD/36176/2007). The authors would like to thank the Flamingo Lodge
447 personnel, Manuel and Cassiano Henriques, Sicopal, PescaSede and Timothy Richardson for
448 help with sample collection in Angola. Steven and Marina Kruger are thanked for the
449 collection of Namibian samples. Gary I Stafford is thanked for the help with the figures.
450

References

Avise JC. 2000. *Phylogeography: the history and formation of species*. Cambridge, Massachusetts, USA. Harvard University Press.

Allendorf FW, Berry O, Ryman N. 2014. So long to genetic diversity, and thanks for all the fish. *Molecular Ecology*. 23:23-25.

Apte S, Gardner JPA. 2002. Population genetic subdivision in the New Zealand greenshell mussel (*Perna canaliculus*) inferred from single-strand conformation polymorphism analysis of mitochondrial DNA. *Molecular Ecology*. 11:1617-1628.

Archangi B, Chand V, Mather PB. 2009. Isolation and characterization of 15 polymorphic microsatellite DNA loci from *Argyrosomus japonicus* (mulloway) a new aquaculture species in Australia. *Molecular Ecology Resources*. 9:412-414.

Bandelt HJ, Forster P, Rohl A. 1999. Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*. 16:37-48.

Beckensteiner J, Kaplan D., Potts WM, Santos CV, O'Farrell MR. 2016. Data-limited population status evaluation of two coastal fishes in southern Angola using recreational catch length-frequency data. *Plos One*. 11:e0147834.

Belkhir K, Borsa P, Chiki L, Refaust N, Bonhomme F. 2000. GENETIX 4.0.1, logiciel sous Windows pour la génétique des populations. Laboratoire Génome Populations Interactions Université de Montpellier.

Briggs JC. 2011. Marine extinctions and conservation. *Marine Biology*. 158:485-488.

Bowen BW, Muss A, Rocha LA, Grant WS. 2006. Shallow mtDNA coalescence in Atlantic pigmy angelfish (genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *Journal of Heredity* 97:1-12.

Canino MF, O'Reilly PT, Hauser L, Bentzen P. 2005. Genetic differentiation in walleye pollock (*Theragra chalcogramma*) in response to selection at the pantophysin (PanI)

476 locus. *Canadian Journal of Fisheries and Aquatic Sciences*. 62:2519-2529.
477 Carvalho GR, Hauser L. 1994. Molecular genetics and the stock concept in fisheries. *Reviews*
478 *in Fish Biology and Fisheries*. 4:326-350.
479 Chapuis M-P, Estoup A. 2007. Microsatellite null alleles and estimation of population
480 differentiation. *Molecular Biology and Evolution*. 24:621-631.
481 Clark PU, Dyke AS, Shakun JD, Carlson AE, Clark J, Wohlfarth B, Mitrovica JX, Hostetler
482 SW, McCabe AM. 2009. The Last Glacial Maximum. *Science*. 325:710-714.
483 Coleman RR, Gaither MR, Kimokeo B, Stanton FG, Bowen BW, Toonen RJ. 2014. Large-
484 scale introduction of the Indo-Pacific damselfish *Abudefduf vaigiensis* into Hawai'i
485 promotes genetic swamping of the endemic congener *A. abdominalis*. *Molecular*
486 *Ecology*. 23:5552-5565.
487 Cornuet JM, Piry S, Luikart G, Estoup A, Solignac M. 1999. New methods employing
488 multilocus to select or exclude populations as origins of individuals. *Genetics*.
489 153:1989-2000.
490 Crawford NG. 2010. smogd: software for the measurement of genetic diversity. *Molecular*
491 *Ecology Resources*. 10:556-557.
492 Diaz-Jaimes P, Uribe-Alcocer M, Rocha-Olivares A, Garcia-de-Leon FJ, Nortmoon P,
493 Durand JD. 2010. Global phylogeography of the dolphinfish (*Coryphaena hippurus*):
494 The influence of large effective population size and recent dispersal on the divergence
495 of a marine pelagic cosmopolitan species. *Molecular Phylogenetics and Evolution*.
496 57:1209-1218.
497 Do C, Waples RS, Peel D, Macbeth GM, Tillett BJ, Ovenden JR. 2014. NEESTIMATOR v2:
498 re-implementation of software for the estimation of contemporary effective
499 population size (Ne) from genetic data. *Molecular Ecology Resources*. 14:209-214.

500 Donaldson KA. Wilson RR. 1999. Amphi-panamic geminates of snook (Percoidei:
501 Centropomidae) provide a calibration of the divergence rate in the mitochondrial
502 DNA central region of fishes. *Molecular Phylogenetics and Evolution*. 13:208-213.
503 Drummond AJ, Rambaut A, 2007. BEAST: Bayesian evolutionary analysis by sampling
504 trees. *BMC Evolutionary Biology*. 7:214-221.
505 Earl DA, von Holdt, BM. 2012. STRUCTURE HARVESTER: a website and progrma for
506 visualizing STRUCTURE output and implementing the Evanno method.
507 *Conservation Genetics Resources*. 4:359-361.
508 Edworthy C, James NC, Potts WM. Submitted. Metabolic structure and variation throughout
509 early development of *Argyrosomus japonicus. African Journal of Marine Science.*
510 Evanno G, Regnaut S, Goudet J. 2005. Detecting the number of clusters of individuals using
511 the software STRUCTURE: a simulation study. *Molecular Ecology*. 14:2611-2620.
512 Excoffier L, Laval G, Schneider S. 2005. Arlequin (version 3.0): An integrated software
513 package for population genetics data analysis. *Evolutionary Bioinformatics*. 1:47-50.
514 Faria R, Weiss S, Alexandrino P. 2012. Comparative phylogeography and demographic
515 history of European shads (*Alosa alosa* and *A. fallax*) inferred from mitochondrial
516 DNA. *BMC Evolutionary Biology*. 12.
517 Francisco SM, Faria C, Lengkeek W, Vieira MN, Velasco EM, Almada VC. 2011.
518 Phylogeography of the shanny *Lipophrys pholis* (Pisces: Blenniidae) in the NE
519 Atlantic records signs of major expansion event older than the last glaciation. *Journal*
520 *of Experimental Marine Biology and Ecology*. 403:14-20.
521 Frankham R. 2005. Stress and adaptation in conservation genetics. *Journal of Evolutionary*
522 *Biology*. 18:750-755.
523 Fu YX, 1997. Statistical tests of neutrality of mutations against population growth
524 hitchhiking and background selection. *Genetics*. 147:915-925.

525 Galarza JA, Carreras-Carbonell J, Macpherson E, Pascual M, Roques S, Turner GF. Rico C.
526 2009. The influence of oceanographic fronts and early-life-history traits on
527 connectivity among littoral fish species. *Proceedings of the National Academy of*
528 *Sciences of the United States of America*. 106:1473-1478.
529 Garroway CJ, Bowman J, Holloway GL, Malcolm JR, Wilson PJ. 2011. The genetic
530 signature of rapid range expansion by flying squirrels in response to contemporary
531 climate warming. *Global Change Biology*. 17:1760-1769.
532 Goudet J. 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. *Journal*
533 *of Heredity*. 86:485-486.
534 Grant WS, Bowen BW. 2006. Living in a tilted world: climate change and geography limit
535 speciation in Old World anchovies (*Engraulis* Engraulidae). *Biological Journal of the*
536 *Linnean Society*. 88:673-689.
537 Griffiths MH. 1996. Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off
538 the east coast of South Africa. *South African Journal of Marine Science-Suid-*
539 *Afrikaanse Tydskrif Vir Seewetenskap*. 17:135-154.
540 Griffiths MH, Heemstra PC. 1995. A contribution to the taxonomy of the marine fish genus
541 *Argyrosomus* (Perciformes: Sciaenidae) with description of two new species from
542 southern Africa. *Ichthyological Bulletin of the JLB Smith Institute of Ichthyologyn* 1-
543 40.
544 Hall T. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis
545 program for Windows 95/98/NT. *Nucleic Acids Symposium Series*. 41: 95-98.
546 Available at: http://www.mbio.ncsu.edu/BioEdit/bioedit.html
547 Henriques R, Potts WM, Santos CV, Sauer WHH, Shaw PW. 2014. Population connectivity
548 and phylogeography of a coastal fish *Atractoscion aequidens* (Sciaenidae) across the
549 Benguela Current Region: evidence of an ancient vicariant event. *Plos One*. 9:e87907.

550 Henriques R, Potts WM, Sauer WHH, Shaw PW. 2012. Evidence of deep genetic divergence
551 between populations of an important recreational fishery species *Lichia amia* L. 1758
552 around southern Africa. *African Journal of Marine Science*. 34:585-591.
553 Henriques R, Potts WM, Sauer WHH, Shaw PW. 2015. Incipient genetic isolation of a
554 temperate migratory coastal sciaenid fish (*Argyrosomus inodorus*) within the
555 Benguela Cold Current system. *Marine Biology Research*. 11:423-429.
556 Henriques R, von der Heyden S, Lipinski MR, du Toit N, Kainge P, Bloomer P, Matthee CA.
557 2016. Spatio-temporal genetic structure and the effects of long-term fishing in two
558 partially sympatric offshore demersal fishes. *Molecular Ecology*. 25:5843-5861.
559 Henriques R, Nielsen ES, Durholtz D, Japp DW, von der Heyden S. 2017. Genetic population
560 sub-structuring of kingklip (*Genypterus capensi*s – Ophidiidae) a commercially
561 exploited demersal fish off South Africa. *Fisheries Research*. 187:86-95.
562 Hill JK, Griffiths HM, Thomas CD. 2011. Climate change and evolutionary adaptations at
563 species' range margins. *Annual Review of Entomology* 56:143-159.
564 Hobday AJ, Pecl GT. 2014. Identification of global marine hotspots: sentinels for change and
565 vanguards for adaptation action. *Reviews in Fish Biology and Fisheries*. 24:415-425.
566 Holtzhausen JA, Kirchner CH, Voges SF. 2001. Observations on the linefish resources of
567 Namibia 1990-2000 with special reference to West Coast steenbras and silver kob.
568 *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap*.
569 23:135-144.
570 Jahn B, Donner B, Muller PJ, Rohl U, Schneider RR, Wefer G. 2003. Pleistocene variations
571 in dust input and marine productivity in the northern Benguela Current: Evidence of
572 evolution of global glacial-interglacial cycles. *Palaeogeography Palaeoclimatology*
573 *Palaeoecology*. 193:515-533.

574 Jost L. 2008. G_{ST} and its relatives do not measure differentiation. *Molecular Ecology*.
575 17:4015–4026.
576 Kirkman SP, Blamey L, Lamont T, Field JG, Bianchi G, Huggett JA, Hutchings L, Jackson-
577 Veitch J, Jarre A, Lett C, Lipinski MR, Mafwila SW, Pfaff MC, Samaai T, Shannon
578 LJ, Shin YJ, van der Lingen CD, Yemane D. 2016. Spatial characterisation of the
579 Benguela ecosystem for ecosystem-based management. *African Journal of Marine*
580 *Science*. 38:7-22.
581 Kirst GJ, Schneider RR, Muller PJ, von Storch I, Wefer G. 1999. Late Quaternary
582 temperature variability in the Benguela Current System derived from alkenones.
583 *Quaternary Research*. 52:92-103.
584 Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, Pecl G. 2011. Long-term
585 shifts in abundance and distribution of a temperate fish fauna: a response to climate
586 change and fishing practices. *Global Ecology and Biogeography*. 20:58-72.
587 Latch EK, Dharmarajan G, Glaubitz JC, Rhodes Jr OE. 2006. Relative performance of
588 Bayesian clustering software for inferring population substructure and individual
589 assignment at low levels of population differentiation. *Conservation Genetics*. 7:295-
590 302.
591 Luiz JO, Madin JS, Robertson DR, Rocha LA, Wirtz P, Floeter SR. 2012. Ecological traits
592 influencing range expansion across large oceanic dispersal barriers: insights from
593 tropical Atlantic reef fishes. *Proceedings of the Royal Society B*. 279:1033-1040.
594 Matthee CA, Cockcroft AC, Gopal K, von der Heyden S. 2007. Mitochondrial DNA variation
595 of the west-coast rock lobster *Jasus lalandii*: marked genetic diversity differences
596 among sampling sites. *Marine and Freshwater Research*. 58:1130-1135.

McKeown N.J Arkhipkin A Shaw P.W 2015. Integrating genetic and otolith microchemistry data to understand population structure in the Patagonian Hoki (*Macruronus magellanicus*). *Fisheries Research*. 164: 1-7.

Miethe T, Dytham C, Dieckmann U, Pitchford JW. 2010. Marine reserves and the evolutionary effects of fishing on size at maturation. *Ices Journal of Marine Science*. 67:412-425.

Monteiro PMS, van der Plas AK, Melice JL, Florenchie P. 2008. Interannual hypoxia variability in a coastal upwelling system: Ocean-shelf exchange climate and ecosystem-state implications. *Deep-Sea Research Part I-Oceanographic Research Papers*. 55:435-450.

Mullen SP, Little K, Draud M, Brozek J, Itzkowitz M. 2012. Hybridization among Caribbean damselfish species correlates with habitat degradation. *Journal of Experimental Marine Biology and Ecology*. 416:221-229.

Nei M, Li WH. 1973. Linkage disequilibrium in subdivided populations. *Genetics*. 75:213-219.

Pauly D, Watson R, Alder J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical Transactions of the Royal Society B-Biological Sciences*. 360:5-12.

Pinsky ML, Palumbi SR. 2014. Meta-analysis reveals lower genetic diversity in overfished populations. *Molecular Ecology*. 23:29-39.

Poll M. 1954. Résultats scientifiques de l'expédition océanographie belge dans les eaux côtières africaines de l'Atlantique sud (1948–1949). IV. Téléostéens acanthoptérygiens (1ère partie). *Institute royal des Sciences naturelles de Belgique* 4: 1-390.

621 Posada D. 2008. jModelTest: Phylogenetic model averaging. *Molecular Biology and*
622 *Evolution*. 25:1253-1256.
623 Potts WM, Childs AR, Sauer WHH, Duarte ADC. 2009. Characteristics and economic
624 contribution of a developing recreational fishery in southern Angola. *Fisheries*
625 *Management and Ecology*. 16:14-20.
626 Potts WM, Henriques R, Santos CV, Munnik K, Ansorge I, Dufois F, Booth AJ, Kirchner C,
627 Sauer WHH, Shaw PW. 2014. Ocean warming a rapid distributional shift and the
628 hybridization of a coastal fish species. *Global Change Biology*. 20:2765-2777.
629 Potts WM, Sauer WHH, Henriques R, Sequesseque S, Santos CV, Shaw PW. 2010. The
630 biology life history and management needs of a large sciaenid fish *Argyrosomus*
631 *coronus* in Angola. *African Journal of Marine Science*. 32:247-258.
632 Pritchard JK, Stephens M, Donnelly P. 2000. Inference of population structure using
633 multilocus genotype data. *Genetics*. 155:945-959.
634 Pusack TJ, Christie MR, Johnson DW, Stallings CD, Hixon MA. 2014. Spatial and temporal
635 patterns of larval dispersal in a coral-reef fish metapopulation: evidence of variable
636 reproductive success. *Molecular Ecology*. 23:3396-3408.
637 Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014. Tracer v1.6. Available from
638 http://beast.bio.ed.ac.uk/Tracer
639 Raymond M, Rousset F 1995. GENEPOP (version-1.2): Population genetics software for
640 exact tests and ecumenicism. *Journal of Heredity*. 86:248-249.
641 Riccioni G, Landi M, Ferrara G, Milano I, Cariani A, Zane L, Sella M, Barbujani G, Tinti F.
642 2010. Spatio-temporal population structuring and genetic diversity retention in
643 depleted Atlantic Bluefin tuna of the Mediterranean Sea. *Proceedings of the National*
644 *Academy of Sciences of the United States of America*. 107:2102-2107.

645 Roberts DG, Gray CA, West RJ, Ayre DJ. 2009. Evolutionary impacts of hybridization and
646 interspecific gene flow on an obligately estuarine fish. *Journal of Evolutionary*
647 *Biology*. 22:27-35.
648 Roberts DG, Gray CA, West RJ, Ayre DJ. 2010. Marine genetic swamping: hybrids replace
649 an obligately estuarine fish. *Molecular Ecology*. 19:508-520.
650 Ryman N, Palm S. 2006. POWSIM: a computer program for assessing statistical power when
651 testing for genetic differentiation. *Molecular Ecology Notes*. 6:600-602.
652 Sala E, Knowlton N. 2006. Global marine biodiversity trends. *Annual Review of Environment*
653 *and Resources*. 31:93-122.
654 Sambrook J, Fritscher EF, Maniatis T. 1989. *Molecular cloning: a laboratory manual*. New
655 York: Cold Spring Harbor Laboratory Press.
656 Silberschneider V, Gray CA. 2008. Synopsis of biological fisheries and aquaculture-related
657 information on mulloway *Argyrosomus japonicus* (Pisces : Sciaenidae) with particular
658 reference to Australia. *Journal of Applied Ichthyology*. 24:7-17.
659 Tamura K, Nei M. 1993. Estimation of the number of nucleotide substitutions in the control
660 region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and*
661 *Evolution*. 10:512-526.
662 Tajima F. 1989. Stastical method for testing the neutral mutation hypothesis by DNA
663 polymorphism. *Genetics*. 123:585-595.
664 Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The CLUSTAL_X
665 windows interface: flexible strategies for multiple sequence alignment aided by
666 quality analysis tools. *Nucleic Acids Research*. 25:4876-4882.
667 van Oosterhout C, Weetman D, Hutchinson WF. 2006. Estimation and adjustment of
668 microsatellite null alleles in nonequilibrium populations. *Molecular Ecology Notes*.
669 6:255-256.

670 von der Heyden S, Bowie RCK, Prochazka K, Bloomer P, Crane NL, Bernardi G. 2011.
671 Phylogeographic patterns and cryptic speciation across oceanographic barriers in
672 South African intertidal fishes. *Journal of Evolutionary Biology*. 24:2505-2519.
673 von der Heyden S, Lipinski MR, Matthee CA. 2007. Mitochondrial DNA analyses of the
674 Cape hakes reveal an expanding panmictic population for *Merluccius capensis* and
675 population structuring for mature fish in *Merluccius paradoxus*. *Molecular*
676 *Phylogenetics and Evolution*. 42:517-527.
677 von der Heyden S, Lipinski MR, Matthee CA. 2010. Remarkably low mtDNA control region
678 diversity in an abundant demersal fish. *Molecular Phylogenetics and Evolution*.
679 55:1183-1188.
680 von der Heyden S, Prochazka K, Bowie RCK. 2008. Significant population structure and
681 asymmetric gene flow patterns amidst expanding populations of *Clinus cottoides*
682 (Perciformes Clinidae): application of molecular data to marine conservation planning
683 in South Africa. *Molecular Ecology*. 17:4812-4826.
684 Waples RS, Do C. 2010. Linkage disequilibrium estimates of contemporary Ne using highly
685 variable genetic markers: a largely untapped resource for applied conservation and.
686 *Evolutionary Applications*. 3:244-262.
687 Weir BS, Cockerham CC. 1984. Estimating *F*-statistics for the analysis of population
688 structure. *Evolution*. 38: 1358–1370
689

690 **Tables**

691 **Table 1:** Mitochondrial genetic diversity and neutrality tests for *A. coronus* CR: N – number
692 of individuals; n – number of haplotypes; PH – number of private haplotypes; *h* – haplotype
693 diversity; π - nucleotide diversity; D – Tajima neutrality test; F_S – Fu neutrality test.
694 Statistically significant results ($p<0.05$) in bold. See Figure 1 for sample site locations (CR
695 accession numbers JX191938-97).

	HEN	**CUN**	**FLA**	**LUC**	**LUA**	**Overall**
N	12	12	12	12	12	60
n	11	12	11	10	11	47
PH	7	11	7	8	7	41
h	0.985	1.000	0.985	0.970	0.985	0.990
π	0.011	0.014	0.010	0.012	0.008	0.010
D	-0.437	-0.976	-0.823	-0.504	-0.917	**-1.501**
Fs	**-5.206**	**-6.652**	**-5.957**	**-3.065**	**-8.853**	**-25.445**

696

697

698 **Table 2:** Genetic diversity in *A. coronus* at six cross-specific microsatellite loci (see Figure 1
699 for site locations): N – number of individuals genotyped; Na – number of alleles; AR – allelic
700 richness (minimum of 16 individuals); H_E – expected heterozygosity; H_O – observed
701 heterozygosity; F_{IS} – inbreeding coefficient. No significant deviations to Hardy-Weinberg
702 were detected (after correction for multiple tests).

Locus	**Measure**	**HEN**	**CUN**	**FLA**	**LUC**	**LUA**	**Overall**
UBA5	**N**	40	26	40	34	40	180
	Na	6	6	7	6	5	9

	AR	5.610	6.000	6.529	5.945	4.999	8.933
	H_E	0.721	0.761	0.724	0.747	0.732	0.743
	H_O	0.775	0.615	0.700	0.853	0.925	0.783
	F_{IS}	-0.063	0.210	0.045	-0.127	-0.252	-0.054
UBA40	**N**	40	26	40	34	40	180
	Na	15	16	14	15	14	22
	AR	13.457	16.000	12.433	14.030	12.264	21.833
	H_E	0.865	0.880	0.842	0.892	0.835	0.879
	H_O	0.825	0.808	0.825	0.971	0.950	0.872
	F_{IS}	0.059	0.102	0.033	-0.073	-0.125	0.008
UBA50	**N**	40	26	39	34	39	178
	Na	16	13	15	15	17	22
	AR	14.585	13.000	13.929	13.755	15.478	21.887
	H_E	0.884	0.875	0.882	0.888	0.894	0.903
	H_O	0.875	0.846	0.821	0.794	0.846	0.843
	F_{IS}	0.024	0.053	0.083	0.121	0.066	0.067
UBA91	**N**	40	26	40	33	34	179
	Na	5	4	4	3	3	6
	AR	4.260	4.000	3.530	2.958	2.650	5.999
	H_E	0.287	0.270	0.282	0.219	0.258	0.293
	H_O	0.275	0.308	0.325	0.182	0.226	0.263
	F_{IS}	0.054	-0.120	-0.139	0.183	0.142	0.105
UBA853	**N**	39	26	35	34	40	174
	Na	9	13	9	11	11	16

	AR	8.323	13.00	8.929	10.465	10.352	16.000
	H_E	0.870	0.878	0.849	0.848	0.830	0.858
	H_O	0.795	0.962	0.943	0.735	0.800	0.822
	F_{IS}	0.028	-0.076	-0.096	0.148	0.049	0.043
UBA854	**N**	40	26	40	34	40	180
	Na	9	7	8	8	6	13
	AR	7.790	7.000	7.167	7.516	5.867	12.833
	H_E	0.717	0.719	0.734	0.742	0.704	0.738
	H_O	0.700	0.654	0.625	0.706	0.900	0.711
	F_{IS}	0.039	0.146	0.161	0.064	-0.267	0.036
Average all loci	**N**	40	26	39	34	39	178
	Na	10	10	10	10	9	15
	AR	9.004	9.833	8.753	9.112	6.768	14.581
	H_E	0.724	0.731	0.718	0.728	0.709	0.734
	H_O	0.698	0.699	0.707	0.697	0.778	0.716
	F_{IS}	0.022	0.069	0.030	0.037	-0.080	0.028

Table 3: Pairwise genetic differentiation between samples of *A. coronus*: mtDNA CR ϕ_{ST} below diagonal, microsatellite F_{ST}/D above diagonal. No values were significantly greater than zero (p>0.05).

	HEN	**CUN**	**FLA**	**LUC**	**LUA**
HEN	-	-	-0.003 / 0.000	0.005 / 0.007	-0.001 / 0.000
CUN	0.017	-	-	-	-

FLA	-0.039	0.018	-	0.002 / 0.008	-0.001 / 0.001
LUC	0.013	0.028	0.028	-	0.001 / 0.001
LUA	0.032	0.015	-0.024	0.021	-

Table 4: Hierarchical analyses of molecular variance (AMOVA) based on frequencies of mtDNA CR haplotypes and nuclear microsatellite multi-locus genotypes for two hypotheses of population sub-structuring: the position of the ABFZ (ABFZ) and the year of sampling (Year). F = fixation index; p = statistical significance.

		mtDNA			**Microsatellites**		
Hypothesis	**Source of variation**	**% of variation**	**F**	**p**	**% of variation**	**F**	**p**
ABFZ	Between groups	0.00	0.000	0.702	0.00	0.000	0.602
	Among sites	2.16	0.021	0.106	0.00	0.000	0.514
	Within sites	98.63	0.014	0.129	100	0.000	0.593
Year	Among groups	0.00	0.000	0.398	0.00	0.000	0.883
	Among sites	1.95	0.019	0.209	0.13	0.001	0.374
	Within sites	98.39	0.016	0.127	99.87	0.000	0.598

Figures

Figure 1: Sampling strategy for *A. coronus* across the northern Benguela sub-system, highlighting sampling sites: Luanda (LUA, N = 40); Lucira (LUC, N = 40); Flamingo River (FLA, N = 40); Cunene River Mouth (CUN, N = 28); Henties Bay (HEN, N = 40). Major oceanographic features of the system: the Benguela and Angola Currents, position of the Angola-Benguela Frontal Zone, and continental shelf width (grey line = -200m contour).

Figure 2: Reconstructed haplotype network for *A. coronus* across the northern Benguela sub-system, based on 524bp of mtDNA CR sequence. Black dots represent missing haplotypes. Sample sites abbreviations as per Figure 1. Branch lenghts are proportional to mutational changes.

Figure 3: Factorial Component Analysis for *A. coronus* microsatellite genotypes. The first two axes explained 11.28% of variation. Sample sites abbreviations as per Figure 1.

Figure 4: Mismatch distribution analyses for *A. coronus*, based on 524bp of mtDNA CR sequence, including neutrality tests (Tajima´s *D* and Fu's F_S) and mismatch distribution parameters (σ - time since expansion in mutation units; θ_0 – population size before expansion; θ_1 – population size after expansion, *T* – time since expansion, KY).

Figure 5: Bayesian Skyline Plot (BSP) showing changes in modelled female effective population size (N_{ef}) over time (KY) in modeled population size for *A. coronus* in the ABFZ region per mutation rate used: A – 3.6% per MY; B - 5% per MY; C – 10% per MY. Solid black line indicates the median estimate, with the 95% HPD lines depicted in grey.

742